

Diversity and dynamics of late Neogene and Quaternary mammalian communities in the Aegean area

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Abstract. The Aegean area is fairly rich in mammal localities for the interval from the Turolian to the Biharian (MN 11 to MN 21). Statistical analyses of faunal lists from 72 localities allow us to observe patterns of diversity and dynamics of mammalian communities in the area. In this paper, the diversity of genera and species, and the rates of appearances and extinctions were calculated for each MN unit. Moreover, the Aegean area has been subdivided into three sectors, and the rate of newly common genera and species during each MN unit was calculated in order to quantify faunal exchanges within the Aegean realm. The relationships of these results to palaeogeographic, tectonic and climatic events are discussed.

Key words: diversity, biogeography, appearance, extinction, mammals, Neogene, Quaternary, Greece, Turkey.

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I. INTRODUCTION

During the last two decades, knowledge of the Neogene mammalian faunas of Greece and Turkey has increased considerably, thanks to great efforts by several laboratories and teams and to international collaborations in palaeontology. Thus, several dozen mammal localities have been discovered, and systematic studies have been carried out. At present it is possible to list more than one hundred late Neogene and early Quaternary mammal localities in these countries. For most of them, systematic studies on faunas and/or on some groups of mammals are published, or at least reliable faunal lists are available. Despite this rich data set, no work has been done on the diversity and bioevents in the mammalian communities of the Aegean realm. In the hope of increasing the value of this rich documentation of the systematics of Neogene and early Quaternary mammals assembled by palaeontologists for more than a century, we have undertaken the present statistical analyses.

This study presents statistical analyses of the later Neogene and early Quaternary mammalian associations known from Greece and Turkey. The time interval concerned covers part of the late Miocene, the Pliocene and the early Pleistocene. These periods overlap European continental stages from the Turolian to the Biharian, or the MN units from MN 11 to MN 21 (Table I). The Neogene mammal units (MN units or MN zones) initially proposed by MEIN (1975, 1989) have recently

Table I

Chronology and regional distribution of Late Miocene to early Pleistocene mammal localities in the Aegean area. The area divided into three sectors: continental Greece (A), Aegean islands + western Turkey (B) and central Anatolia (C) according their past and present particularities in faunas and environments (see text)

PERIOD	STAGE	MN	AGE in MA	SECTORS			
				A	B		C
				W. GREECE	E. GREECE	W. TURKEY	C. TURKEY
PLEIS- TOCENE	BIHARIAN	21	1.4	Volos			Emirkaya 2
		20	1.8	Zeli 2A + B Megalopolis Megalopolis TH2	Kalymnos		
		19	2.0	Tourkobounia 2 Kaiafa			
PLIOCENE	VILLANYIAN	18	2.2	Pyrgos Megalopolis TH1 Kastoria 2	Lagkada		Sinap sup.
		17	2.6	Rema Aslan	Wolaks Kardamena		Kamisli Y. Sögütönü
		16	3.0	Tourkobounia 1 Limni 6 Kastoria 1 Karabourun	Kalavarda Damatria Archipolis		Gülyazi
	RUSCINIAN	15	4.0	Spilia 3 + 4 Ptolemais 3 Ptolemais 1	Apolakkia 2		Çalta
		14	5.0	Kardia Limni 3 Spilia 1 Spilia 0 Trilophos	Karpathos Maritsa	Develi	Elbistan Babadat Akçaköy İgdeli
		13	6.5	Monasteri Ano Metochi 3 Dytiko Ano Metochi 2 Maramena		Amasya Bayırköy Gülpınar	Kavurca Kinik
		12	8.0	Rema Marmara Pikermi(Chomat.) Pikermi	Samos L5 Samos L4		Kemiklitepe A+B Garkin
MIOCENE	TUROLIAN	11	9.0	Vathylakkos Lefkon Prochoma	Samos Q4		Mahmutgazi Kemiklitepe D Dendil Kayadibi
	VALLESIAN	10		Biodrak			Kaleköy

been reviewed by DE BRUIJN et al. (1992), who proposed some adjustments and corrections. According to these authors, the last stage of the Neogene (Villanyian) includes MN units 16 and 17, but not 18. On the other hand, VAN DER MEULEN & KOLFSCHOTEN (1986) included MN18 in the late Villanyian since the faunas from the type area of the Villanyian (localities Villány 3 and Villány 5) cannot be attributed to the Pleistocene.

The database for this work is provided by the faunal lists published by SICKENBERG et al. (1975), GAZIRY (1976), SCHMIDT-KITTLER (1976), DE BRUIJN (1976, 1989), DE BRUIJN & VAN DER

MEULEN (1975), STAESCHE & SONDAAR (1979), ENGESSER (1980), BLACK et al. (1980), SOLOUNIAS (1981), ÜNAY & DE BRUIJN (1984), VAN DER MEULEN & KOLFSCHOTEN (1986), KÖHLER (1987), DE BONIS et al. (1988), SEN (1977, 1982, 1991, 1994), SEN et al. (1989, 1991, 1994), SÜMENGİN et al. (1990), MONTUIRE et al. (1994) and DE BONIS et al. (1994). The geographic positions of these mammal localities are shown in Fig. 1, and their chronology in Table I. In this table are listed 72 mammalian faunas covering the latest Vallesian-Biharian time interval.

A study such as this requires a time frame with precise chronologic boundaries. First of all, we retained age and MN zone correlations for mammal localities, when available and/or reliable, such as they were proposed by the authors who studied the faunas. There is no suitable zonation based on mammalian faunas of the Neogene and Quaternary peculiar to the Aegean realm. In general, the mammal localities of this area are correlated with the European Neogene Mammal Chronology and MN zones. We are aware of some problems with these correlations because of regional particularities of the mammal faunas in the Aegean realm, and of difficulties of correlation with the European mammal ages and MN zones, since these were mainly erected on the basis of west

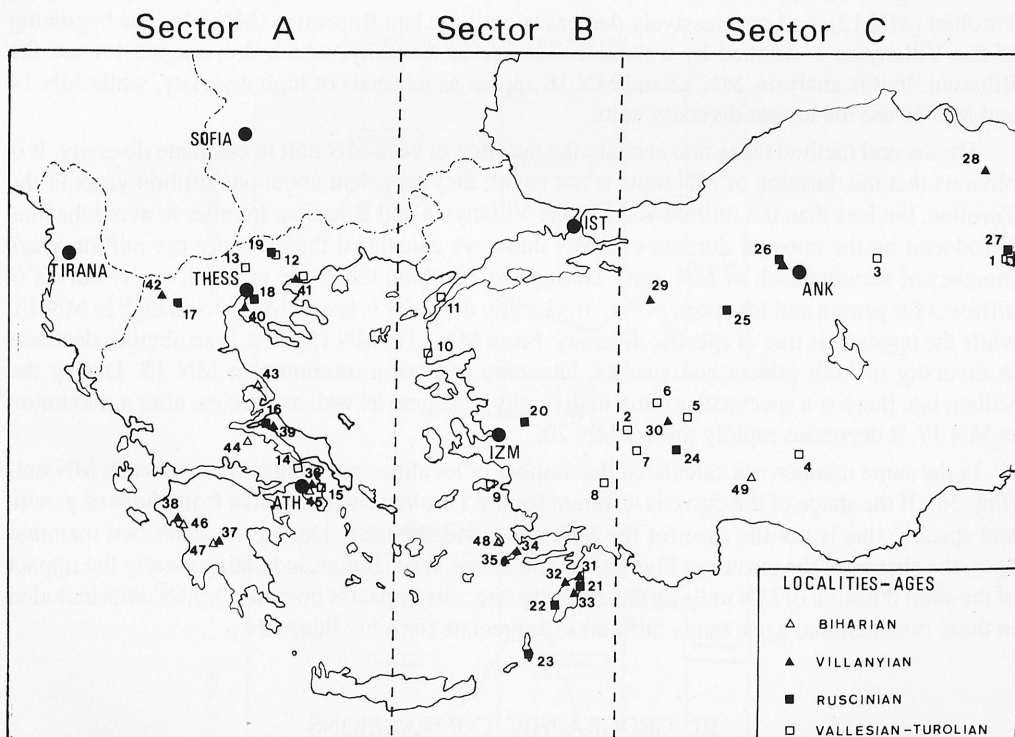


Fig. 1. Locations of the late Neogene mammal localities mentioned in this paper. The Aegean area is divided in three sectors: west (A), central (B) and east (C). The numbers indicate the following localities: 1. Kaleköy and Dendil, 2. Kemiklitepe A, B, D, 3. Kavrurca, 4. Kayadibi, 5. Garkin, 6. Kinik, 7. Mahmutgazi, 8. Amasya, 9. Samos Quarries, 10. Gülpınar, 11. Bayırköy, 12. Maramena, Lefkon, Ano Metochi 2-3 and Monasteri, 13. Prochoma, Vathylakkos and Dytiko, 14. Biodrak, 15. Pikermi and Chomateri, 16. Limni 3, 17. Kardina and Ptolemais 1+3, 18. Trilophos, 19. Spilia 0,1,3 and 4, 20. Develi, 21. Maritsa, 22. Apolakkia, 23. Karpathos, 24. Akçaköy, 25. Babadat, 26. Çalta, 27. Iğdeli, 28. Kamisli, 29. Yukari Söğütönü, 30. Gülyazi, 31. Damatria, 32. Kalavarda, 33. Archipolis, 34. Lagkada, 35. Kardamena, 36. Tourkobounia 1, 37. Megalopolis TH1, 38. Pyrgos, 39. Limni 6, 40. Karaburun, 41. Rema Marmara, Rema Aslan, 42. Kastoria, 43. Volos, 44. Zeli 2, 45. Tourkobounia 2, 46. Kaifa, 47. Megalopolis TH2, 48. Kalymnos, 49. Emirkaya 2.

European localities and mammal faunas. However, this chronology remains the most useful thanks to the comparison of common elements in faunas from western, central and southeastern Europe. The absolute ages of the European Neogene mammal ages and MN unit boundaries are after STEININGER et al. (1989).

II. TAXONOMIC DIVERSITY

Taxonomic diversity was calculated for genera as well as for species. This parameter can be analysed in two different ways: by counting the number of genera or species recorded in each MN unit, or by calculating the number of occurrences per million years (Ma).

Fig. 2 presents the curves of generic diversity (a), specific diversity (b) and number of sites (c) as recorded in each MN unit. For each MN unit, the numbers of genera or species are indicated, and then connected to form the curves. It can be observed that the curves of genera and species are very similar, and that their diversities do not seem to be related to the number of sites, since the curve in Fig. 2c is notably different from the two previous ones. Diversity is high during the middle Turolian (MN 12), and progressively decreases until the late Ruscinian (MN 14). The beginning of the Villanyian is marked by a notable increase in diversity, which drops again toward the Biharian. In this analysis, MN 12 and MN 16 appear as intervals of high diversity, while MN 14 and MN 19 are the lowest diversity units.

The second method takes into account the duration of each MN unit to calculate diversity. It is obvious that the duration of MN units is not equal; they represent about one million years in the Turolian, but less than 0.5 million years in the Villanyian and Biharian. In order to avoid the bias introduced by the unequal durations of MN units, we calculated the diversity per million years (number of taxa/duration of MN unit). During the Turolian, the shape of the diversity curves is different for genera and for species (Fig. 3). Generic diversity is low in MN 12 and high in MN 13, while the opposite is true of specific diversity. From MN 13 to MN 15, there is an obvious decrease in diversity of both genera and species. Diversity reaches a minimum in MN 15. During the Villanyian, there is a spectacular jump in diversity of genera as well as species; after a maximum in MN 17, it decreases rapidly toward MN 20.

In the same manner, we calculated the number of localities per million years in each MN unit (Fig. 3c). If the shape of the curve is different for the Turolian and Ruscinian from those of genera and species, this is not the case for the Villanyian and Biharian. During the latter two mammal ages, the shapes of the curves in Figs 3a, 3b and 3c are very similar, indicating clearly the impact of the short duration of MN units on the diversity rate; this impact is obvious for MN units included in these two mammal ages, but is difficult to appreciate for other intervals.

III. GEOGRAPHIC COMPARISONS

Methods and objectives

Taking into account the past and present day geographies and environments of the Aegean realm, we propose to divide it into three sectors: continental Greece (A), Aegean islands + Western Turkey (B) and Central Anatolia (C) (Fig. 1; Table I). These three sectors, as approximately delimited in Fig. 1, are at present differentiated by their geographic, topographic, climatic and ecological characteristics. Present day faunal dispersal is clearly indicative: the western sector has more faunal elements in common with Central and western Europe than the eastern one (ONDRIAS 1966; KUMERLOEVE 1975). On the other hand, the extant faunas of the Anatolian platform have several Asiatic and African components. Their Neogene mammal faunas also show, if individual

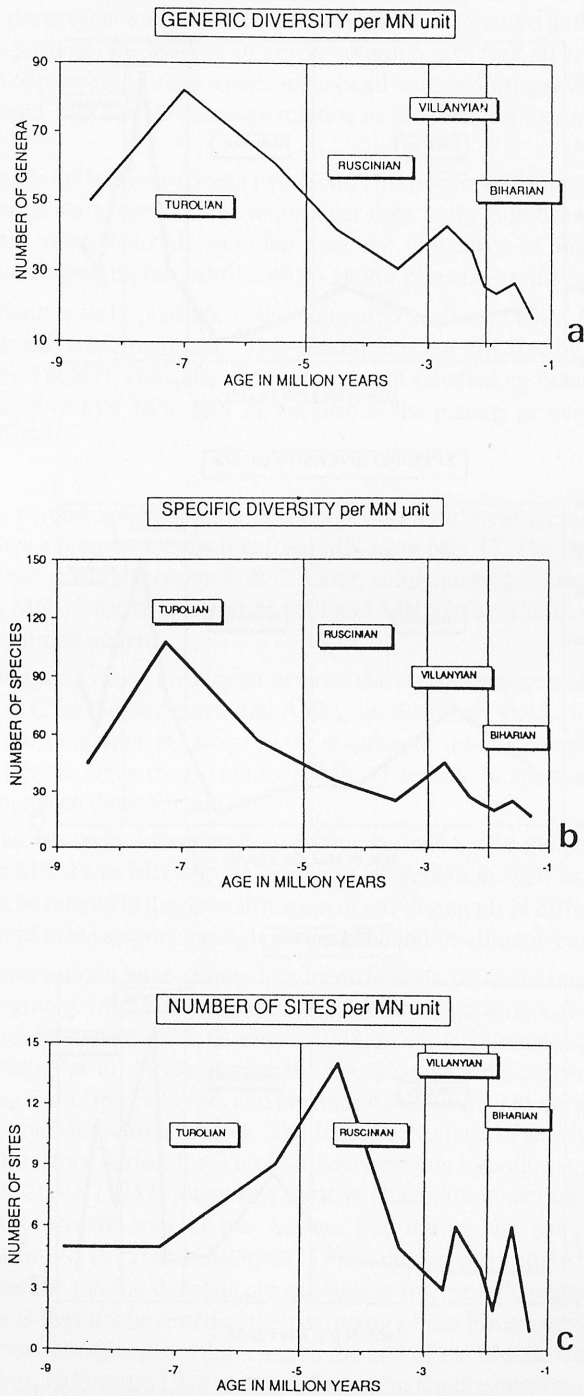


Fig. 2. Diagrams of generic (a) and specific (b) diversity in each MN unit, and their relationship to the number of mammal localities (c).

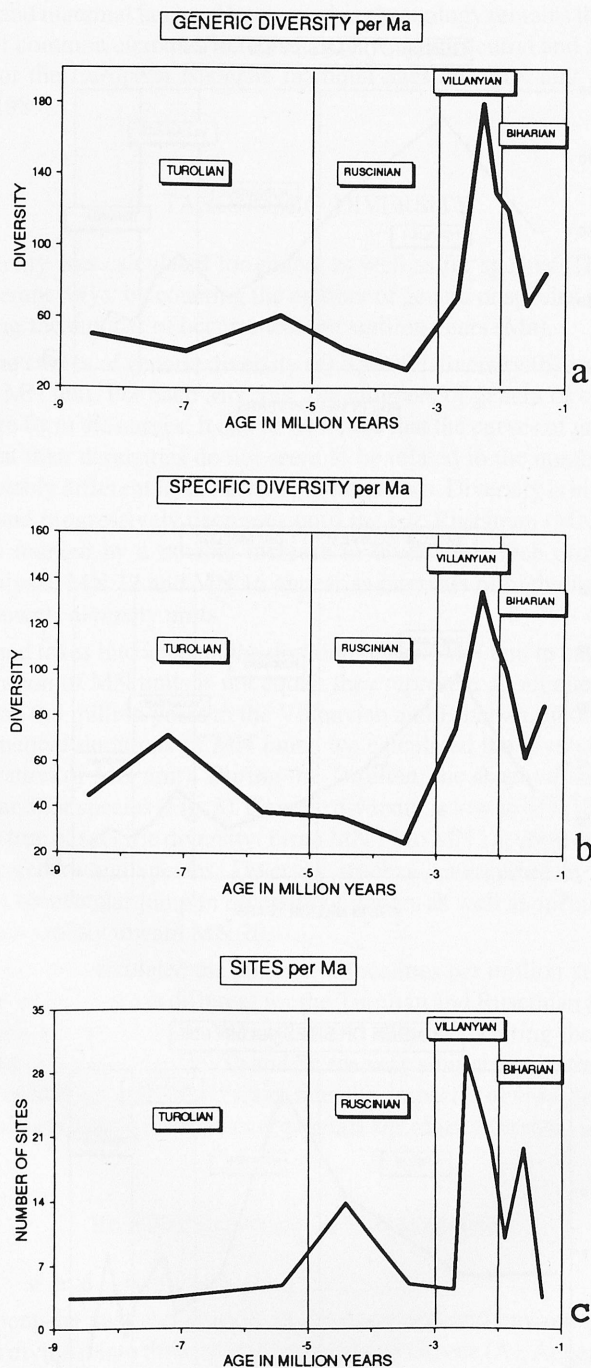


Fig. 3. Diagrams of generic and specific diversity per million years (Ma), and their relationships to the frequency of mammal localities per Ma. Taxonomic diversity, as well as the number of mammal localities, is expressed as number per Ma. a) Generic diversity per Ma. b) Specific diversity per Ma. c) Number of localities per Ma. The importance of the number of localities attributed to an MN unit is obtained by dividing the number of localities by the duration of the MN unit.

faunas from two different sectors are compared, some obvious differences in composition (SEN 1982). The aim of the present analysis is to quantify these differences and their variation in time and space. For this purpose, the number of newly common taxa (not all common taxa in order to avoid the influence of panchronic taxa which occur in all sectors during several MN units) between two sectors is counted, and their percentage relative to the total number of taxa is calculated for each MN unit.

The importance of similarities between two sectors in an MN unit is interpreted as being related to the degree of faunal exchange. The variation over time in the number of newly common taxa and their percentage relative to all recorded taxa are indicative of faunal movements; their correlations with palaeogeographic modifications and/or climatic events are investigated.

Such a comparison is only possible if the compared sectors contain faunas of similar ages, including both large and small mammals. This condition is not satisfied by some sectors for some intervals of time (see Table I). Thus, the comparison is not satisfactory between sectors A & C and B & C for the interval of MN 16 to MN 21 because of the paucity or even absence of adequate faunas in Central Turkey.

R e s u l t s

Fig. 4 shows the percent newly common genera between different sectors. Between all sectors, this proportion shows a progressive decline from MN 12 to MN 17. The decline is sharp between A & B and A & C, but smooth between B & C. Later, some intervals of time, such as MN 18 and MN 20 for A & B, MN 17 for B & C and MN 18 and MN 21 for A & C, appear to have a large number of newly common genera.

The results at the species level are similar to those shown by the genera (Fig. 5). The comparisons between sectors B & C on the one hand, and A & C on the other, yield diagrams that are almost identical to the generic diagrams; the shape of the diagram of species comparison between sectors A & B is a little different, since the period from MN 11 to MN 16 appears to favour continuous specific exchange between these sectors.

These results can be easily interpreted given our knowledge of the palaeogeography of the Aegean area. From MN 11 to MN 16, the exchange of genera as well as species progressively diminished; this can be related to the diversification of environments in different sectors of the area or to some isolation of these sectors through geographic and/or climatic barriers.

Geodynamic observations have resulted in identification of some important changes in the Neogene palaeogeography of the Aegean area. According to palaeogeographic studies (KERAUDREN 1975; LUTTIG & STEFFENS 1976; GUERNET 1978; RÖGL & STEININGER 1984; KOJUMDGIEVA 1987; ORSZAG-SPERBER et al. 1993), during the late Miocene, the Aegean realm constitutes a continuous landmass from Greece to Iran and beyond; it is delimited to the north by the Paratethys and to the south by the Mediterranean Sea. The large percentage of newly common genera and species between all sectors during the Turolian supports this hypothesis. RÖGL & STEININGER (1984) and KOJUMDGIEVA (1987) suggest a narrow channel connecting the Paratethys to the Mediterranean in the present area of the Aegean Sea during the late Miocene (Tortonian). According to KERAUDREN (1975) and GUERNET (1978), this seaway cannot be demonstrated, since outcrops of late Miocene marine deposits are missing in the central Aegean. Thus, they suggest that the Aegean Sea is first documented at the beginning of the Pliocene, when the central sector is invaded by a marine transgression which marks the end of the Messinian crisis in the Mediterranean area. Moreover, GUERNET (1978) proposed a northward progressive opening of the Aegean marine basin during the Pliocene, consequent on extensional movements and faulting.

According to palaeomagnetic data and their geodynamic interpretations, the Greek peninsula has rotated clockwise about 25° since the beginning of the Pliocene, its pivot being situated in the southern part of the former Yugoslavia (LAJ et al. 1982; KISSEL et al. 1986; KISSEL & LAJ 1988;

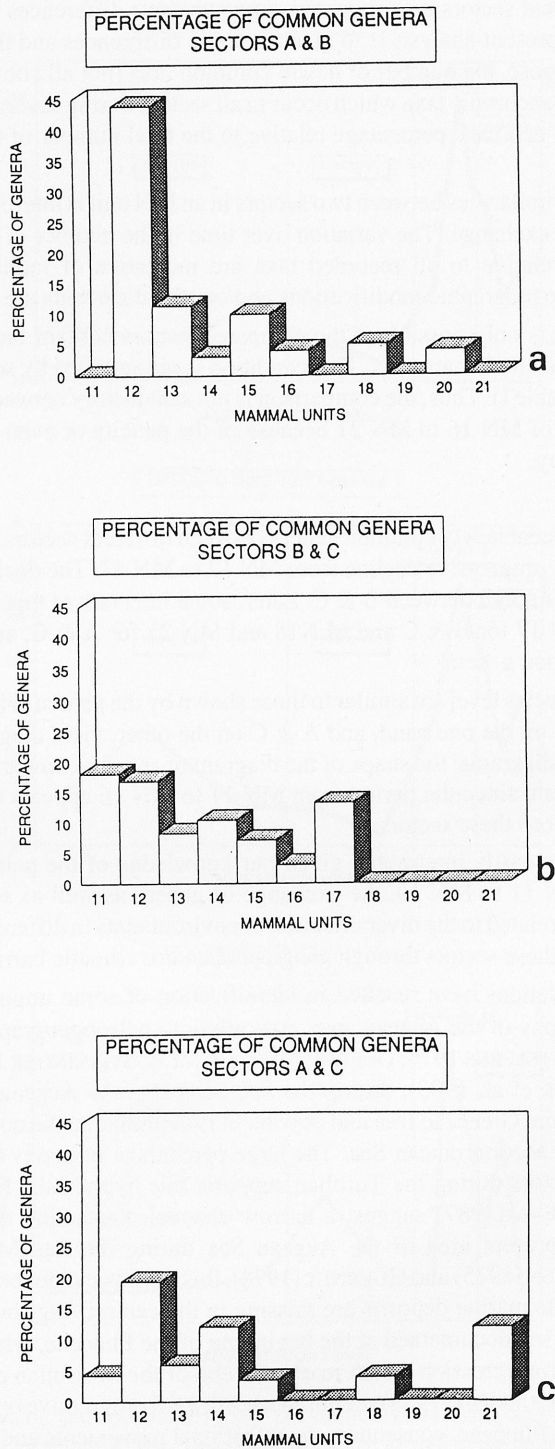


Fig. 4. Percentage of newly common genera between sectors A-B (a), B-C (b) and A-C (c) for each MN unit from the Turolian to the Biharian (see also Fig. 1 and Table I).

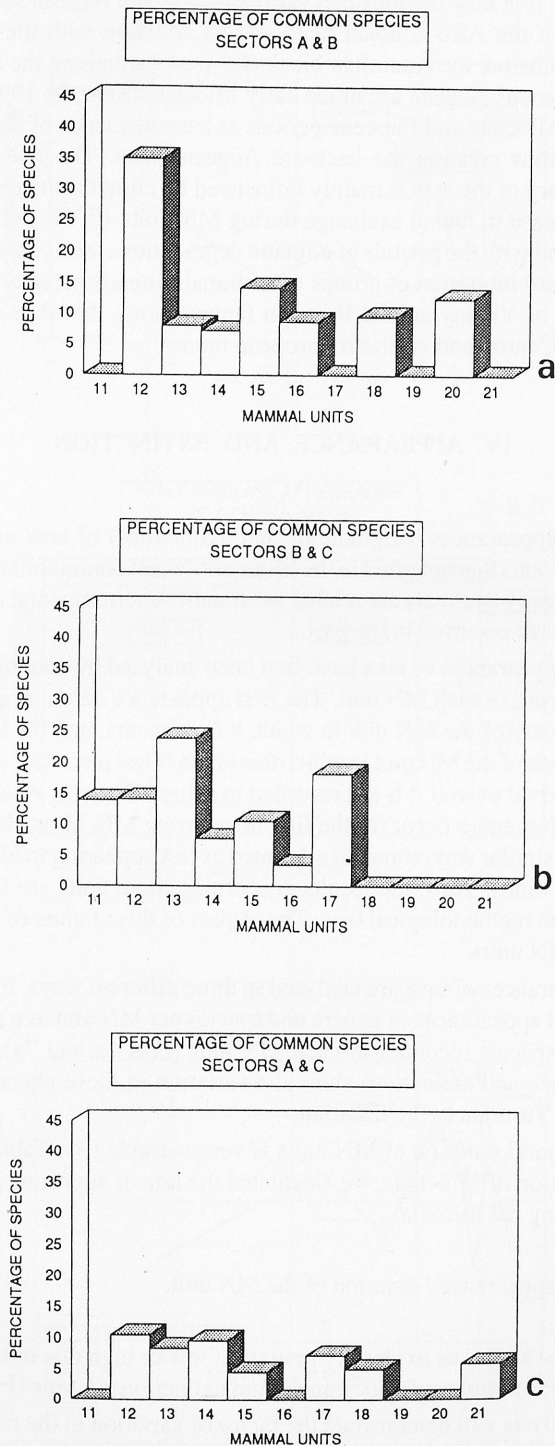


Fig. 5. Percentage of newly common species between sectors A-B (a), B-C (b) and A-C (c) for each MN unit from the Turolian to the Biharian (see also Fig. 1 and Table I).

KONDOPOULOU 1993). It is now obvious that the opening of the Aegean seaway is related to the northwestern motion of the Afro-Arabian plate and its collision with the Eurasian plate. As a consequence of this collision, the Anatolian block slid westward along the North Anatolian fault system, creating the famous Aegean arc in the early Miocene (SENGÖR 1992). This arc migrated southward during the Miocene and Pliocene periods as a consequence of the westward motion of the Anatolian block, thus creating the back-arc Aegean basin. The late Pliocene-Pleistocene palaeogeographic history of the area is mainly influenced by climatic changes and their effects on the sea level. The increase in faunal exchange during MN units 17, 18 and 20 between different sectors can be correlated with the periods of climatic degradation – and consequent sea level drops – which led to southward migration of groups of mammals already present in northern countries. A close consideration of Villanyian and Biharian faunas shows that they contain many taxa in common with several Central and northern European faunas.

IV. APPEARANCE AND EXTINCTION

M e t h o d o l o g y

The first and last appearances (originations and extinctions) of taxa are of great interest to illuminate biological events that occurred in the history of faunal communities; it can be postulated, and then tested, that these bio-events are related to climatic, environmental and palaeogeographic modifications which have occurred in the past.

The first and last appearances of taxa have first been analysed by counting the number of taxa appearing or disappearing in each MN unit. The first appearance datum of a taxon is taken as the age of the lower boundary of the MN unit in which it first occurs, and the last appearance datum is the upper boundary age of the MN unit in which this taxon is last recorded; the taxon is considered present during this interval even if it is not recorded in some MN units. An artifact of this method is that some taxa which seem to occur for the first time during MN 11 or MN 12 may in fact have originated earlier; in a similar way, some taxa counted as last appearing in MN 20 and MN 21 may have survived in later times. Thus, the results concerning these units are obviously incomplete, since they include some methodological bias. The impact of this manner of counting is much less or even nil for other MN units.

First and last appearances of taxa are analysed in three different ways. First, we calculated the number of first and last appearances of genera and species per MN unit as a percentage of the total number of genera or species recorded in each MN unit (Figs 6a and 7a). The curves of these percentages (appearance and extinction) show the variation in these phenomena in mammalian communities from the Turolian to the Biharian.

However, the temporal duration of MN units is very variable (see Table I). In order to avoid the impact of the duration of MN units, we calculated the rate of appearances and extinctions per million years (Ma) using the formula:

percent first (last) appearance / duration of the MN unit.

This second method allows us to identify periods of low or high rate of renewal of faunas, and shows more clearly the dynamics of appearances and extinctions in time (Figs 6b and 7b).

A third type of analysis will demonstrate the factor of variation in the rate of appearances and extinctions from one MN unit to the next (Figs 6c and 7c), as obtained by the formula:

factor of variation = $\text{Rate}_{\text{MnN}} / \text{Rate}_{\text{MnN-1}}$

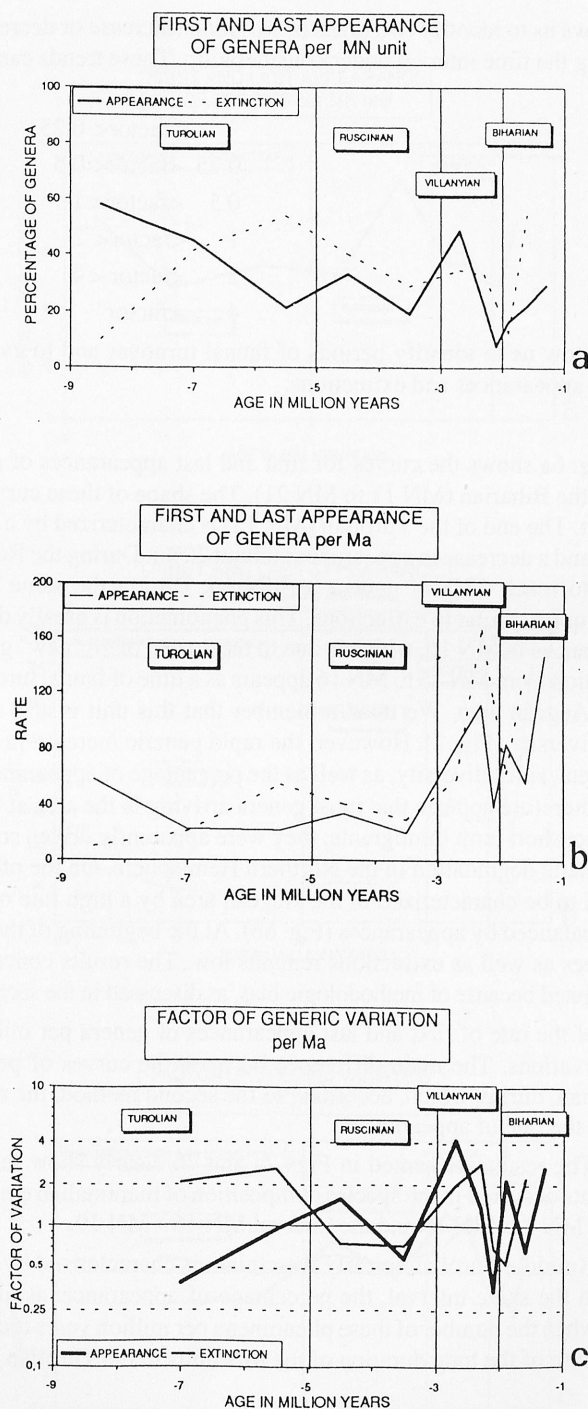


Fig. 6. Diagrams of first and last appearance of genera per MN unit (a), per million years (b), and their factor of variation (c). The percentages are relative to the total number of genera present in each MN unit. These values are subdivided by the duration of the MN unit to obtain the rate of these phenomena per million years. The factor of variation is obtained by the formula $Y = \text{Rate}_{\text{MNn}} / \text{Rate}_{\text{MNn-1}}$.

This formula allows us to identify two types of variation (increase or decrease) in appearances and extinctions during the time interval under consideration. These trends can be subdivided into six categories as:

strong decrease	factor < 0.25
average decrease	0.25 < factor < 0.5
weak decrease	0.5 < factor < 1
weak increase	1 < factor < 2
average increase	2 < factor < 4
strong increase	4 < factor

These analyses allow us to identify periods of faunal turnover and to evaluate the temporal dependence between appearances and extinctions.

R e s u l t s

G e n e r a. Fig. 6a shows the curves for first and last appearances of genera per MN unit from the Turolian to the Biharian (MN 11 to MN 21). The shape of these curves is different from one period to the next. The end of the Turolian (MN 13) is characterized by a substantial increase in extinctions (55%) and a decrease in appearances (about 20%). During the Ruscinian, extinctions gradually decrease, to reach 27% of genera in MN 15. During the same stage, the curve of appearances remains quite similar to extinctions. This phenomenon is greatly disturbed by the high percentage of appearances in MN 16, which is due to the arrival of 18 "new" genera in the Aegean area. Thus, the transition from MN 15 to MN 16 appears as a time of faunal turnover in mammalian communities of the Aegean area. We must remember that this unit is also characterized by an increase in generic diversity (Fig. 2). However, the rapid generic increase in MN 16 seems to be a temporally brief event, since diversity, as well as the percentage of appearances, drops at the end of the Villanyian. It therefore appears that most genera arriving in the area at the beginning of the Villanyian were in fact short term immigrants; they were apparently driven southward because of the late Pliocene climatic degradation in the Northern Hemisphere. On the other hand, the end of the Villanyian seems to be characterized in the Aegean area by a high rate of generic extinction which is not counterbalanced by appearances (Fig. 6b). At the beginning of the Biharian (MN 19), the rate of appearances as well as extinctions remains low. The results concerning the later MN units cannot be interpreted because of methodologic bias, as discussed in the section on methodology.

The calculation of the rate of first and last appearances of genera per million years (Fig. 6b) confirms these observations. The main difference between the curves of percentages and rates concerns the Villanyian, during which, according to the second method, the rate of extinctions in MN 17 is higher than the rate of appearances.

S p e c i e s. The results presented in Figs 7a and 7b clearly show three intervals during which important events occurred in the species composition of mammalian communities: these are the interval MN 12 - MN 14, MN 15 and the interval MN 16 - MN 19.

The first interval (middle Turolian to early Ruscinian) is characterized by high percentages of species extinction. In the same interval, the percentage of appearances is also moderately high (Fig. 7a). However, when the number of these phenomena per million years is calculated, we obtain very low values because of the long duration of the MN units in the Turolian and early Ruscinian (Fig. 7b).

During the late Ruscinian (MN 15), the percentage of appearances increases notably. However, the rate of appearances and extinctions remains very similar to that in MN 14, once more because of the long duration of this unit. Thus, both appearances and extinctions display low rates, indicating a calm period of species renewal in mammalian communities during the Turolian and Ruscinian.

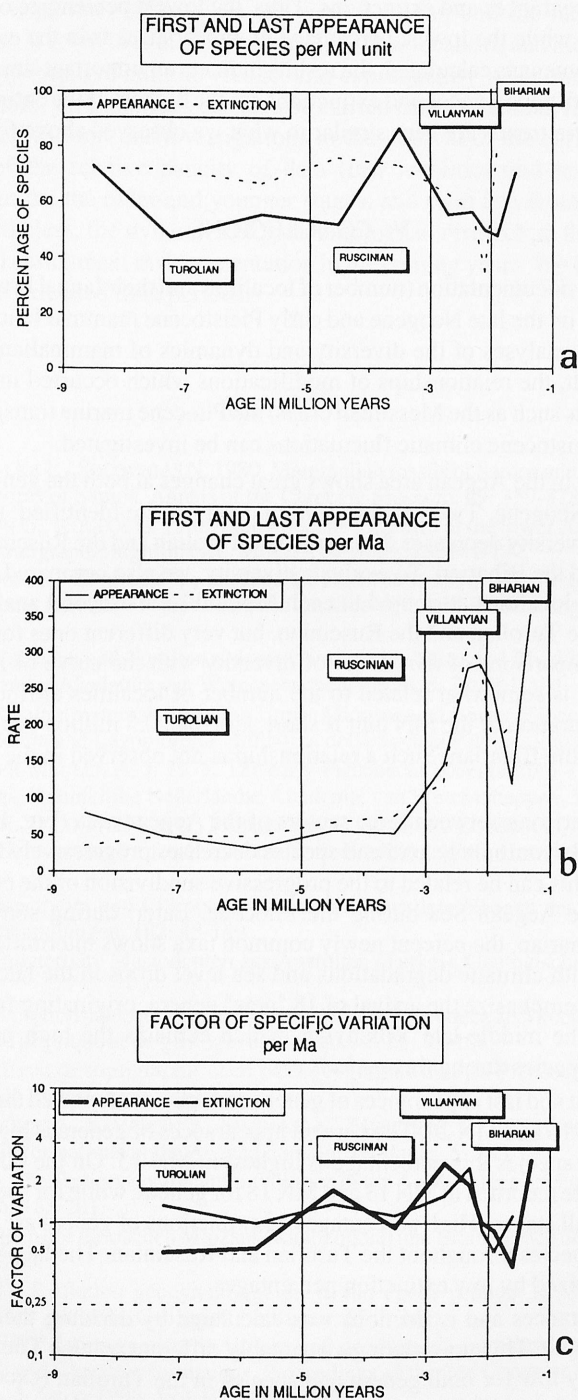


Fig. 7. Diagrams of first and last appearance of species per MN unit (a), per million years (b), and their factor of variation (c). See Fig. 6 for further explanation.

The third interval (Villanyian and early Biharian) is characterized by a continuous decrease in the percentages of appearances and extinctions. Thus, the lowest percentage of extinctions occurs in the late Villanyian, while the lowest percentage of appearances is in the early Biharian. When the rate of these phenomena is calculated, the results indicate an important time of faunal turnover, since the values for both appearances and extinctions are the highest of the entire Turolian-Biharian interval (Fig. 7b). These trends are very similar to what we observed above for genera.

V. CONCLUSIONS

The richness of the documentation (number of localities and their faunal lists, systematic studies and chronologic data) on the late Neogene and early Pleistocene mammal faunas from the Aegean area allows statistical analyses of the diversity and dynamics of mammalian communities to be carried out. As a result, the relationships of modifications which occurred in the composition of faunas to abiotic events such as the Messinian crisis, the Pliocene marine transgression and the late Pliocene and early Pleistocene climatic fluctuations can be investigated.

Mammal diversity in the Aegean area shows great changes at both the generic and the specific level during the late Neogene. Two periods of high diversity are identified: the middle Turolian and the Villanyian. Diversity decreases during the late Turolian and the Ruscinian, and also during the late Villanyian and the Biharian. To evaluate diversity, we also compared the diversity curves with the frequency of localities attributed to each MN unit. This second analysis yielded almost identical results for the Turolian and the Ruscinian, but very different ones for the Villanyian and the Biharian. The comparisons of the curves of diversity with the curve of number of localities showed that diversity is somewhat related to the number of localities attributed to an MN unit, especially when the duration of the MN unit is short, less than 0.5 million years, which is the case in the Villanyian and the Biharian. Such a relationship is not observed in the Turolian-Ruscinian interval.

Geographic comparisons between three sectors of the Aegean area (Fig. 1, Table I) show that the percentage of newly common genera and species decreases progressively from the Turolian to the early Villanyian; this can be related to the progressive subdivision of the continental landmass by the opening of the Aegean Sea during the Pliocene. Later, during some MN units of the Villanyian and the Biharian, the percent newly common taxa shows intermittent increases, which could be correlated with climatic degradations and sea level drops in the late Pliocene and early Pleistocene. We must emphasize the arrival of 18 "new" genera, originating from the north, in the Aegean area during the middle-late Villanyian, which explains the high percentage of newly common genera and species during this period.

The analysis of first and last appearances of genera and species identified three periods of faunal turnover: MN 13, MN 16 and MN 20. The percent appearances of genera is high in MN 12, MN 14 and MN 17, while for species this percentage is highest in MN 15. On the other hand, the lowest percent appearances are recorded in MN 13 and MN 18 for genera, while for species this percentage remains moderate in all stages. High percentages of extinctions of genera are observed in MN 13 and MN 18, and for species throughout the Turolian and Ruscinian. The late Villanyian and early Biharian are characterized by low extinction percentages.

The rate of appearances and extinctions was calculated by dividing the percentages by the duration of each MN unit. This procedure gives notably different results. The rate of appearances and extinctions is very low for both genera and species in the Turolian (except MN 13) and the Ruscinian, but very high in the Villanyian. In fact, these rates seem closely tied to the duration of MN units, since they are low when the MN unit is long, but high when it is short. This methodologic bias partly reduces the value of the results concerning the rate of appearances and extinctions, and, in consequence, their value in shedding light on bioevents in the mammalian communities.

To carry out the present study, we recorded all available and reliable faunal lists from Greece and Turkey for the time interval between the early Turolian and the late Biharian; a total of 72 mammal localities. It is obvious that more data, e. g., new localities and more detailed taxonomic studies, will certainly improve our knowledge, and consequently will complement the results of this paper. Furthermore, such analyses can also be carried out on mammal faunas of older periods. However, we decided to limit our investigations to the interval of the early Turolian to the late Biharian because of the relative paucity of data (few localities and less reliable systematic determinations) from the older and younger stages, and even less from the earlier periods of the Miocene. Nevertheless, the dynamics of palaeontological research in the Aegean area allows us to forecast a rapid enrichment in documentation in the coming years. We then propose to pursue this study over more extended time periods.

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